

THE SYSTEMATICS OF ANNUAL SPECIES OF
MALACOTHRIX (ASTERACEAE: LACTUCEAE)
ENDEMIC TO THE CALIFORNIA ISLANDS

W. S. DAVIS

Department of Biology, University of Louisville,
Louisville, KY 40292

ABSTRACT

A taxonomy based primarily on phenetic evidence is proposed for the annual taxa of *Malacothrix* DC. endemic to the California Islands, California. Field studies, herbarium collections, and growth chamber progenies provided information about chromosome numbers, breeding systems, the presence or absence of isolating mechanisms between taxa, comparative morphology, and distributions. New taxa described are *Malacothrix foliosa* ssp. *crispifolia* ($2n=14$), *M. f.* ssp. *philbrickii* ($2n=14$), *M. f.* ssp. *polycephala* ($2n=14$), and *M. junakii* ($2n=28$). Kept at the species level are *M. indecora* ($2n=14$), *M. insularis* ($2n$ =unknown), and *M. squalida* ($2n=28$). Also discussed are possible relationships between the insular endemics and *Malacothrix coulteri* ($2n=14$) and *M. incana* ($2n=14$), two species that occur both on the California Islands and on the mainland.

Malacothrix DC. comprises annual and herbaceous perennial plants that occur exclusively in the western United States and northern Mexico, except for two species that also occur in Argentina and Chile. The most recent monograph recognized 23 taxa (Williams 1957), and Davis (1993) has updated the taxonomy of taxa occurring in California. During the taxonomic history of the genus, there has been general agreement about the circumscription of a majority of species. Notable exceptions are the annual species endemic to the California Islands, originally published as follows: *Malacothrix foliosa* A. Gray (1886, San Clemente Island); *M. indecora* Greene (1886, Santa Cruz Island); *M. insularis* Greene (1885, Los Coronados Island); and *M. squalida* Greene (1886, Santa Cruz Island). More recently, annual *Malacothrix* also have been collected on Anacapa, San Miguel, San Nicolas, Santa Barbara, and Santa Rosa islands. Most of these collections have been referred to the original four species whose taxonomy has received a variety of treatments. For example, Williams (1957) reduced *M. indecora* and *M. squalida* to varietal rank under *M. foliosa* and combined *M. insularis* with *M. foliosa* var. *foliosa*. Ferris (1958) treated *M. squalida* as a variety of *M. insularis* and retained *M. foliosa* and *M. indecora* as species. Munz (1974) accepted specific status for *M. foliosa* and stated, "Two other spp. have been proposed and variously combined as vars., all of these occurring only on the islands off our coast and to me quite mixed up as to separating characters and distribution."

This study was undertaken to resolve the taxonomic disagreements noted above; its primary focus is on the annual taxa of *Malacothrix* endemic to the California Islands. Also included in the study are two taxa occurring both on the islands and on the mainland. The first is *Malacothrix incana* (Nutt.) Torrey & A. Gray, a diploid ($2n=14$) perennial occurring in sand dune areas of coastal mainland California in Santa Barbara and San Luis Obispo counties. *Malacothrix incana* also is an element of sand dunes on San Miguel, Santa Cruz (not recently seen there), Santa Rosa, and San Nicolas islands. It was included in the study because it is similar to the annual insular endemics in several aspects of floral and leaf morphology. Also included, because of morphological similarities to *M. insularis* and *M. squalida*, is *Malacothrix coulteri* A. Gray, a diploid ($2n=14$) annual occurring in Arizona, California, Nevada, Utah, Argentina, Chile, and northwestern Mexico. It was collected on Santa Cruz and Santa Rosa islands in the past (as *M. coulteri* var. *cognata* Jepson), but not since 1932.

Initial findings of consistent patterns of morphological and physiological variation within the study group (henceforth referred to as the *M. foliosa* complex) developed from studies of growth chamber progenies grown under similar light, temperature, and soil conditions (see Davis and Philbrick 1986 for propagation methods). Voucher specimens are deposited in Davies Herbarium (DHL), University of Louisville. Progenies grown from wild achenes of all taxa except *Malacothrix insularis* Greene were available, as well as progenies from self-pollinations, intrataxon pollinations, and intertaxon pollinations.

For breeding system determinations, a plant was considered to be self-incompatible if no pigmented/filled achenes were produced from at least three self-pollinations or in undisturbed heads, and if crosses with other plants of the same taxon produced normal numbers of pigmented/filled achenes.

No information regarding the presence of self-compatible or self-incompatible plants in natural populations was gathered because no island trip was longer than four days, and ten days are required for fruit set to occur following pollination. Pollination systems appeared to be very effective in all natural populations, and high percentages of full/pigmented achenes were noted in all taxa during collections of achenes in the field. On San Clemente Island, for example, mature flower heads of *Malacothrix foliosa* ssp. *foliosa* were collected from 14 different plants. Percentages of full/pigmented achenes per head were 95–100, and the potential numbers of achenes per head were 39–112. In natural populations, insects are the most important pollinators for all taxa, and a study on San Miguel Island by Miller and Davis (1985) found that flower heads of *Malacothrix incana* are visited by a suite of generalist bees, small beetles, true bugs,

and a few flies. The most frequently seen pollinator was *Agapostemon texanus* Cresson. The large metallic-green female was often found crawling all over the large flower heads. This same pollinator was seen on both *M. foliosa* ssp. *polycephala* and *M. incana* on San Nicolas Island during a study of hybridization between the two species.

The presence or absence of isolating mechanisms between taxa was investigated experimentally in growth chamber progenies by comparing the results from intrataxon crosses with those from intertaxon crosses with respect to the following: quantity and quality of fruit set, percentage seed germination, patterns of seedling growth and development, percentage stainable pollen, and chromosomal associations at diplonema, diakinesis, and metaphase I of meiosis.

Field studies were conducted during visits to Anacapa Island (1982, 1992), San Clemente Island (1985), San Miguel Island (1984), San Nicolas Island (1984–1988, 1993), Santa Barbara Island (1982), and Santa Cruz Island (1985, 1991).

Morphological data were collected from herbarium specimens deposited in the following herbaria: CAS, DAV, DS, GH, JEPS, K, LA, LAM, MO, ND, NDG, NY, OBI, POM, RSA, SBBG, SBM, SD, TEX, UC, UCSB, UNM, US. All of the collections of *Malacothrix* cited in Raven (1963), Foreman (1967), Philbrick (1972), Wallace (1985), and Junak et. al. (1995) were analyzed.

The taxonomy proposed in this paper is based primarily on phenetic evidence. Cluster analysis of 33 quantitative floral and vegetative characters (Fig. 1) provided a picture of over-all resemblances between taxa in the study, and assisted in making taxonomic decisions. Cluster methods were performed on a personal computer using NTSYS-PC, version 1.6 (Rohlf 1990). A similarity matrix was constructed using the product-moment correlation method on unstandardized mean values, and the phenogram was obtained using the unweighted pair-group arithmetic averages method (UPGMA).

A summary of the new classification of the plants covered in the study is given in Table 1, together with the old classification and brief information about distributions, reproductive biology, and chromosome numbers (see Fig. 2 for geographic distributions).

All of the taxa grown in growth chamber progenies from wild fruit or fruit from sister crosses within a taxon were true-breeding, and patterns of morphological variation observed in natural populations were comparable to patterns found in growth chamber progenies. The different taxa are most consistently distinguishable on the basis of differences in cauline leaf morphology (Fig. 3) and size differences in some quantitative floral traits (Table 2). Differences between taxa in quantitative floral traits are easily seen in the field and in growth chamber progenies, but are difficult to assess in her-

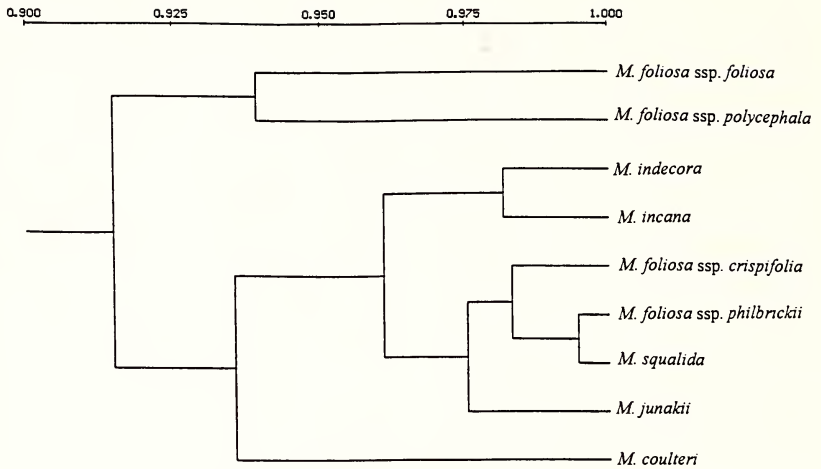


FIG. 1. Phenogram showing the clustering of taxa of the *Malacothrix foliosa* complex resulting from UPGMA cluster analysis carried out on NTSYS (Rohlf 1990) using means of 33 quantitative vegetative and floral traits (scale = correlation coefficients). Cophenetic analysis indicated that the phenogram is a good fit to the original data set. *Malacothrix insularis* was not included because of insufficient data from dried specimens, and no information from living plants.

barium specimens. This may account for some of the taxonomic confusion in the past when few collections were available for study.

Diploid insular endemic taxa comprising only self-compatible, strongly self-pollinating plants (CRI, IND, POL) have shorter corollas, stamens, and involucre than diploid members of the *M. foliosa* complex that comprise both self-compatible and self-incompatible plants (FOL, INC, PHI) (Table 2). In the latter group, I have been unable to find any differences between self-compatible plants and self-incompatible plants. In comparative size of diagnostic quantitative floral traits, FOL, INC, and PHI are similar to other taxa of *Malacothrix* that have been found to comprise outcrossing plants. The polyploid SQU and the presumptive polyploid INS have the general floral dimensions of an outcrosser, but SQU comprises only self-compatible, self-pollinating plants. The diploid COU and the polyploid JUN are somewhat intermediate in size between other known inbreeders and outcrossers in some quantitative floral traits (Table 2).

Biological barriers interfering with gene exchange between taxa of the *M. foliosa* complex and other predominately mainland taxa have been found in growth chamber studies. For example, it has been very difficult to obtain filled achenes from cross-pollinations between members of the *M. foliosa* complex (COU, CRI, FOL, INC, IND, JUN, PHI, POL, SQU) and any predominately mainland taxon,

TABLE 1. OLD CLASSIFICATION, AND NEW CLASSIFICATION. DISTRIBUTIONS, BREEDING SYSTEMS, AND CHROMOSOME NUMBERS OF TAXA OF THE *M. FOLIOSA* COMPLEX. Names of taxa are represented in the text by the first three letters of specific or subspecific epithets as listed in column 2. All of the taxa are annuals except *M. incana*.

Old classification	New classification	Distribution	Breeding system	Chromosome number
<i>M. coulteri</i>	<i>M. coulteri</i> (COU)	Mainland; formerly on Santa Cruz & Santa Rosa Islands	Self-compatible & strongly self-pollinating	$2n = 14$
<i>M. foliosa</i>	<i>M. foliosa</i> ssp. <i>crispifolia</i> (CRI)	East & west Anacapa Island	Self-compatible & strongly self-pollinating	$2n = 14$
	<i>M. foliosa</i> ssp. <i>foliosa</i> (FOL)	Widespread on San Clemente Island; formerly on Los Coronados Island	Both self-compatible & self-incompatible	$2n = 14$
	<i>M. foliosa</i> ssp. <i>philbrickii</i> (PHI)	Widespread on Santa Barbara Island	Both self-compatible & self-incompatible	$2n = 14$
	<i>M. foliosa</i> ssp. <i>polycephala</i> (POL)	Widespread on San Nicolas Island	Self-compatible & strongly self-pollinating	$2n = 14$
<i>M. incana</i>	<i>M. incana</i> (INC)	Currently mainland and insular	Self-compatible & self-incompatible	$2n = 14$
<i>M. indecora</i>	<i>M. indecora</i> (IND)	San Miguel, Santa Cruz & Santa Rosa Islands	Self-compatible & moderately self-pollinating	$2n = 14$
<i>M. insularis</i>	<i>M. insularis</i> (INS)	Rare on Los Coronados Island	Not known	Not known
	<i>M. junakii</i> (JUN)	Rare on middle Anacapa Island	Self-compatible and moderately self-pollinating	$2n = 28$
<i>M. squalida</i>	<i>M. squalida</i> (SQU)	Santa Cruz & middle Anacapa Islands	Self-compatible & strongly self-pollinating	$2n = 28$

and few artificial hybrids have been available for study. All hybrids produced have been sterile (pollen stainability generally <10%), and abnormal chromosome associations are generally found in meiosis. Likewise, growth chamber studies have found that intertaxon crosses between predominately mainland taxa also produce hybrids rarely, that these hybrids are sterile (stainable pollen <50%), and that ab-

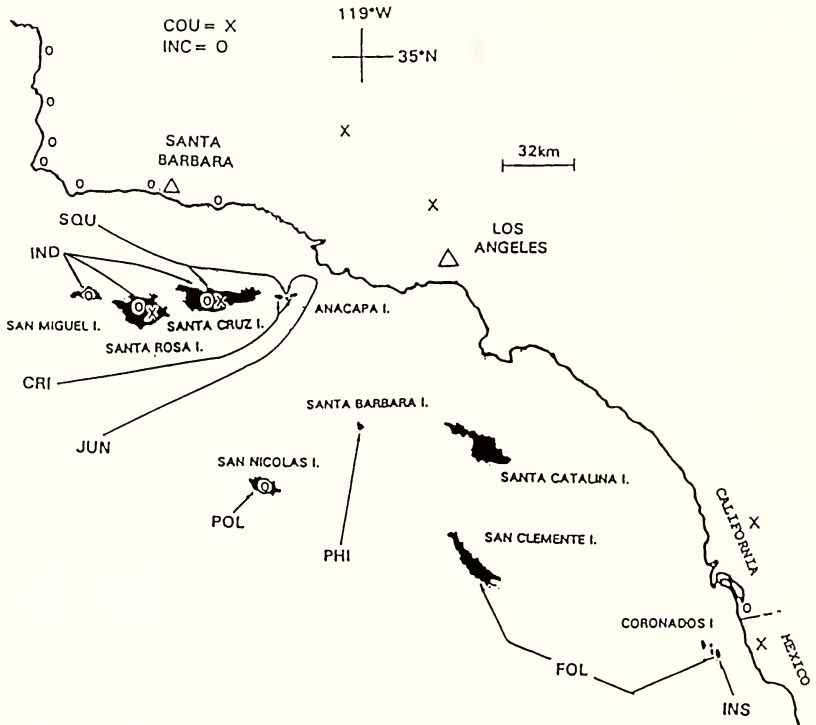


FIG. 2. Distribution of taxa of the *Malacothrix foliosa* complex on the California Islands and adjacent mainland (COU = *M. coulteri*, CRI = *M. foliosa* ssp. *crispifolia*, FOL = *M. f.* ssp. *foliosa*, INC = *M. incana*, IND = *M. indecora*, INS = *M. insularis*, JUN = *M. junakii*, PHI = *M. f.* ssp. *philbrickii*, POL = *M. f.* ssp. *polycephala*, SQU = *M. squalida*).

normal chromosome associations may be found in meiosis (Davis 1993).

In contrast, growth chamber hybridization studies indicate that all but one of the diploid members of the *M. foliosa* complex (CRI, FOL, INC, IND, PHI, POL, but not COU) are generally interfertile. Fruit set was normal in all intertaxon crosses except PHI \times IND where $<5\%$ of the achenes were filled/pigmented in a majority of cases when self-incompatible plants of PHI were used as the female parent (percentage of stainable pollen of F_1 hybrids from PHI \times IND was $>90\%$). Germination rates were normal for seeds from all intertaxon crosses including PHI \times IND, growth and development were apparently normal, a majority of hybrid combinations displayed hybrid vigor, and all growth chamber hybrids flowered normally. Meiosis in all intertaxon hybrids was apparently normal, and chromosome segregation was normal in metaphase I and II. Mean

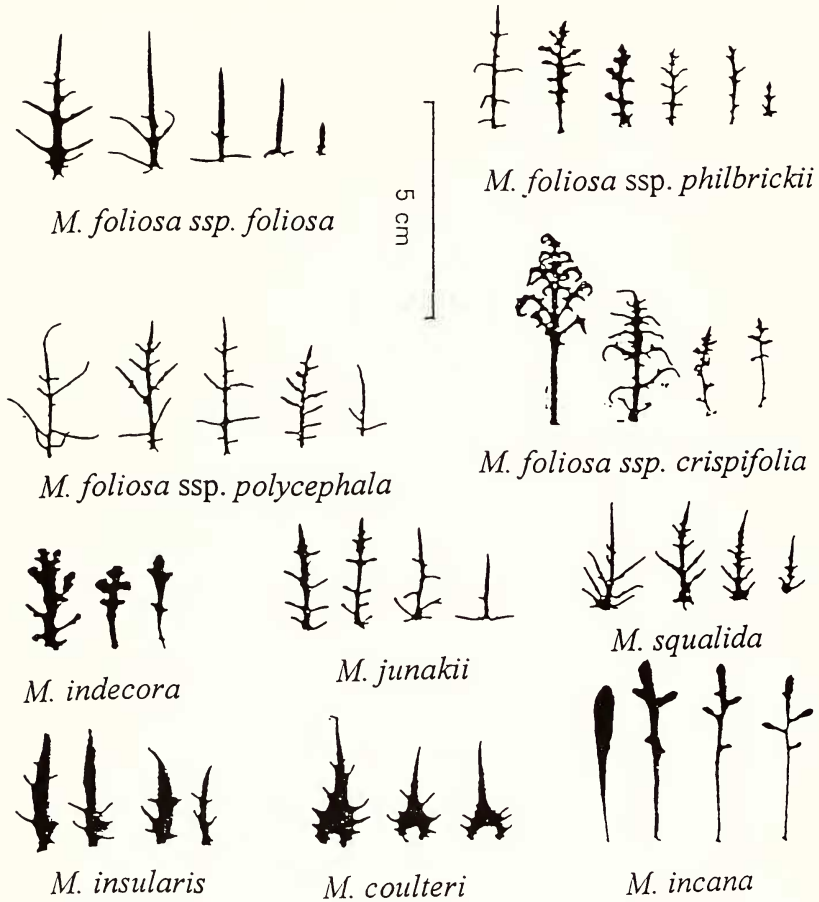


FIG. 3. Silhouettes of cauline leaves of taxa of the *Malacothrix foliosa* complex arranged with progressively more apical leaves to the right.

percentages of stainable pollen in F_1 and F_2 hybrids did not differ significantly ($P > 0.05$, Students t-test) from mean stainable pollen percentages in plants grown from wild fruit or from intrataxon crosses, except in some of the F_1 hybrids from $INC \times IND$ which had stainable pollen $< 40\%$.

In contrast, the two polyploid members of the *M. foliosa* complex (JUN, SQU), and the diploid COU are reproductively isolated from the above diploid taxa of the *M. foliosa* complex and from each other (Table 3).

Geographic isolation or absence of sympatry currently helps preserve the integrity of interfertile taxa of the *M. foliosa* complex. Islands occupied by a single taxon include San Clemente (FOL),

TABLE 2. VARIATION IN QUANTITATIVE FLORAL FEATURES OF TAXA OF THE *M. FOLIOSA* COMPLEX (GIVEN ARE RANGE, MEAN \pm STANDARD DEVIATION; N = NUMBER OF INDIVIDUAL PLANTS STUDIED).

Taxon	Corolla length (mm)	Ligule exertion (mm)	Ligule length (mm)	Ligule width (mm)	Stamen length (mm)
<i>M. coulteri</i>	8.8-12	1.9-5	5.2-7.2	1.3-2	4.8-6.2
N = 6	10.8 \pm 0.8	3.3 \pm 1.1	6.1 \pm 0.8	1.6 \pm 0.3	5.8 \pm 0.6
<i>M. foliosa</i> ssp. <i>crispifolia</i>	6.1-10	2.7-3.9	4.6-6.2	2.2-2.7	4.3-6
N = 16	8.9 \pm 0.8	3.2 \pm 0.3	5.5 \pm 0.7	2.4 \pm 0.2	5.4 \pm 0.4
<i>M. foliosa</i> ssp. <i>foliosa</i>	10-16	4.6-7.9	6.7-12.1	2-4	5.3-8.1
N = 34	12.9 \pm 1.4	6.6 \pm 1.0	8.7 \pm 1.1	3.3 \pm 0.4	6.7 \pm 0.7
<i>M. incana</i>	10.8-20	5.2-9	7.5-12	2.2-3.1	7-12
N = 23	16.46 \pm 1.3	6.7 \pm 1.3	10.0 \pm 0.9	2.9 \pm 0.2	9.8 \pm 1.0
<i>M. indecora</i>	4.5-8	1.3-3.3	2.7-4.6	1.5-2.5	3.4-5.4
N = 28	6.9 \pm 0.8	1.9 \pm 0.5	3.8 \pm 0.5	2.2 \pm 0.2	4.6 \pm 0.5
<i>M. insularis</i>	11.7-15	3.5-5	7.5-9.5	2-2.5	6-9
N = 11	12.3 \pm 1.1	4.6 \pm 0.7	8.4 \pm 0.6	2.2 \pm 0.1	7.5 \pm 0.7
<i>M. jumakii</i>	8.6-10	3.5-5.5	5-6	1.4-2	5.5-6.2
N = 31	9.0 \pm 0.8	3.8 \pm 0.7	5.3 \pm 0.5	1.8 \pm 0.2	5.4 \pm 0.4
<i>M. foliosa</i> ssp. <i>philbrickii</i>	8.3-15.2	3.5-7.3	5-10.8	2-4	5.1-8.2
N = 39	10.7 \pm 0.8	5.1 \pm 0.7	7.1 \pm 0.7	3.2 \pm 0.4	6.2 \pm 0.5
<i>M. foliosa</i> ssp. <i>polycephala</i>	5.3-8.5	2.5-4	3-5.5	1.5-2.7	2.9-5
N = 45	7.4 \pm 1.0	2.9 \pm 0.6	4.7 \pm 0.7	3.1 \pm 0.5	4.1 \pm 0.6
<i>M. squalida</i>	12-18.5	5.8-10.5	8-13	2-3	6.2-9.5
N = 37	16.2 \pm 1.6	8.1 \pm 1.3	10.8 \pm 1.2	2.6 \pm 0.2	7.8 \pm 0.7

TABLE 3. PERCENTAGE OF STAINABLE POLLEN IN F₁ HYBRIDS BETWEEN MEMBERS OF THE *M. FOLIOSA* COMPLEX. COU = *M. coulteri*, JUN = *M. junakii*, SQU = *M. squalida*, FOL/PHI = both *M. foliosa* ssp. *foliosa* and *M. f.* ssp. *philbrickii* as parents (given are range, mean \pm standard deviation, and number of hybrids analysed, N).

	COU	JUN	SQU	FOL/PHI
COU	75-98 92.4 \pm 8.3 N = 8			
JUN		46-100 91.0 \pm 17.3 N = 22		
SQU			55-100 96.5 \pm 9.8 N = 12	
FOL/PHI				85-100 97.8 \pm 1.5 N = 62
	0-42 22.7 \pm 13.9 N = 16	10-32 18.3 \pm 7.0 N = 20		
	0-40 12.5 \pm 10.9 N = 17	2-58 28.4 \pm 17.1 N = 14	12-58 31.4 \pm 14.4 N = 20	

Santa Barbara (PHI), West Anacapa (CRI), and East Anacapa (CRI). Islands where two taxa of the *M. foliosa* complex occur are Middle Anacapa (JUN and SQU), San Miguel (INC and IND), San Nicolas (INC and POL), Santa Cruz (IND and SQU), and Santa Rosa (INC and IND). Both FOL and INS have been collected on the south islet of Los Coronados Island, but the former has not been seen there since 1926, and the few available herbarium specimens of FOL and INS from the island provide no evidence of hybridization. As far as is known, different diploid taxa of the *M. foliosa* complex are not sympatric except on San Miguel Island and San Nicolas Island. In the latter case, INC is a recent addition to the flora and is freely hybridizing with the annual POL (Davis and Junak 1988). This case of natural hybridization between two of the most different diploid taxa of the *M. foliosa* complex is consistent with evidence from growth chamber studies that there is a general lack of biological isolating mechanisms between diploid members of the group, excluding COU. On San Miguel Island, putative hybrids between INC and IND recently have been found, but the situation has not yet been analyzed.

DISCUSSION

This study indicates that six of the diploid members of the *M. foliosa* complex (*Malacothrix foliosa* ssp. *crispifolia*, *M. f.* ssp. *foliosa*, *M. f.* ssp. *philbrickii*, *M. f.* ssp. *polycephala*, *M. incana*, and *M. indecora*, but not *M. coulteri*) are essentially interfertile, and constitute a closely knit group, both morphologically and biogeographically. Morphological differentiation in the group has occurred more rapidly than development of reproductive isolating mecha-

nisms between taxa. This, together with current insular distributions and patterns of morphological differentiation, suggests that adaptive radiation has been involved in the origin of at least some taxa.

In a future report more detailed evidence will be presented to support particular relationships within the *M. foliosa* complex, and specific hypotheses concerning the origins of all of the taxa. However, the hypothesis that self-compatible, self-pollinating *M. f. ssp. polycephala* has been derived from *M. f. ssp. foliosa* is particularly well-supported by morphological, physiological, and biogeographical evidence, and will be briefly discussed here. The two taxa are similar with respect to growth habit, growth rate in cultivation, cauline leaf morphology, involucre structure, achene micromorphology, and habitat preference, but differ consistently with respect to the size of several quantitative floral traits (Table 2). In addition, current island distributions and breeding system evidence from growth chamber studies lend support to the hypothesis that *M. f. ssp. foliosa* was the progenitor and *M. f. ssp. polycephala* the derivative in a process of adaptive radiation that involved dispersal of self-compatible plants of *M. f. ssp. foliosa* from San Clemente Island to San Nicolas Island, fixation of self-compatibility, and selection for reduction in size of floral traits.

In addition, morphological, biogeographical, and chromosomal evidence from this study suggests that the polyploid *M. squalida* is an amphidiploid between *M. foliosa ssp. philbrickii* and *M. coulteri*. Artificial hybrids between the putative parents are sterile (Table 3), and generally indistinguishable from *M. squalida* in critical diagnostic traits. Triploid hybrids between *M. squalida* and *M. coulteri* or *M. foliosa ssp. foliosa* have reduced pollen stainability, and the maximum chromosome association found at diplo-nema of meiosis is 7 pairs and 7 univalents. The current and past distributions of the taxa also are consistent with the hypothesis.

TAXONOMY

Following is a key to the annual taxa of *Malacothrix* endemic to the California Islands.

1. Corollas generally <10 mm long; ligules of outermost florets exerted <4 mm beyond the involucre
 2. Plants generally mat-like, 2–10 cm tall, branched from the base; cauline leaves generally fleshy, margins with 3–8 pairs of short, obtuse, nearly equal lobes; tips of outer phyllaries obtuse (2) *M. indecora*
 - 2' Plants not mat-like, generally 10–30 cm tall, branched from the base or above; cauline leaves not generally fleshy, margins toothed or with narrow, sharp lobes; tips of outer phyllaries acute or broadly acute
 3. Margins of cauline leaves crisped; longest outer phyllaries nearly as long as inner phyllaries; fruit 1.4–1.6 mm long, 15-ribbed and 5-angled; endemic to Anacapa Island (1a) *M. foliosa ssp. crispifolia*
 - 3' Margins of cauline leaves not crisped; longest outer phyllaries generally ca.

- half as long as inner phyllaries; fruit 0.9–1.3 mm long, evenly 15-ribbed; endemic to San Nicolas Island (1d) *M. foliosa* ssp. *polycephala*
- 1' Corollas generally >10 mm long; ligules of outermost florets generally exerted >5 mm beyond the involucre
- 4. Outer phyllaries 20–26, hyaline/scarios margins >0.5 mm wide
 - 5. Fruit with 1–3 smooth, persistent setae; tips of 5 strongest ribs generally not extended above the tips of lesser ribs at achene apex; endemic to Los Coronados Island (3) *M. insularis*
 - 5' Fruit generally without persistent setae; tips of 5 strongest ribs extended beyond the tips of lesser ribs at the achene apex; endemic to Middle Anacapa and Santa Cruz islands (5) *M. squalida*
- 4' Outer phyllaries 9–19, hyaline/scarios margins <0.4 mm wide
 - 6. Fruit without an outer pappus; plants diploid, >70% of stainable pollen 3-pored
 - 7. Stems usually one from a tap-root, branched above, erect; uppermost cauline leaves with 1–3 pairs of long, narrow lobes at the base, the distal 2/3 with entire margins; achene 15-ribbed, ribs generally equal; endemic to San Clemente and Los Coronados islands (1b) *M. foliosa* ssp. *foliosa*
 - 7' Stems one, or more often several from a taproot, branched above, decumbent to erect; margins of uppermost cauline leaves generally evenly toothed or lobed nearly to the apex; fruit 15-ribbed and 5-angled; endemic to Santa Barbara Island (1c) *M. foliosa* ssp. *philbrickii*
 - 6' Fruit with an outer pappus of minute teeth and 1 naked persistent seta; tetraploid ($2n = 28$), >70% of stainable pollen 4-pored; endemic to middle Anacapa Island (4) *M. junakii*

1. *Malacothrix foliosa* A. Gray, Synoptical Flora of North America edition 2. 1²:455. 1886.—Type: USA, California, Los Angeles Co., San Clemente Island, April 1885, *Nevin and Lyon s.n.* (holotype: GH!; isotypes: CAS!, DS!, UC!).

Plants annual from a taproot, 5–50 cm tall. Stems one to several from the base, branched above, decumbent, ascending, or erect, pale green to medium red, essentially glabrous, but arachnoid at leaf axiles. Basal leaves 5–14 cm long, 6–40 mm wide, oblanceolate to narrowly obovate, margins toothed or pinnately lobed or divided, tips broadly acute to attenuate acute; lower cauline leaves like basal leaves but more deeply lobed or divided; uppermost cauline leaves pinnately lobed or divided, tips acute to attenuate acute. Heads 2–7 mm wide at anthesis, base tapered or rounded. Involucre 5–12 mm high; outer phyllaries 7–20, lanceolate to narrowly ovate, 1.5–6.4 mm long, 0.7–2 mm wide, nearly as long or noticeably shorter than the inner pappus, tips acute to broadly acute, green, red-tinged, or red, the midvein and tips generally darker red, hyaline/scarios margins <0.3 mm wide; inner phyllaries 8–22, linear-lanceolate, 5–8 mm long, 0.8–2 mm wide, generally pale to medium green or red-tinged, hyaline/scarios margins <0.3 mm. Receptacle naked. Florets 15–120; corolla 5–17 mm long, light yellow to medium yellow, ligules of outermost florets 2–3 mm wide, exerted 1.5–10 mm beyond the involucre. Stamens 3–8.2 mm long; style branches 0.2–0.7

mm long, fruit 0.9–1.6 mm long, cylindric-fusiform, the base narrower than the constricted, truncate apex, brown to dark brown, equally 15-ribbed, or 5-angled; outer pappus none (very rarely one or two naked, weakly persistent setae). Self-compatible or self-incompatible. $2n=14$.

1a. **Malacothrix foliosa** A. Gray ssp. **crispifolia** W. S. Davis ssp. nov.—TYPE: USA, California, Ventura Co., Anacapa Island, east island, grassy northeast-facing slope, east of Lighthouse, 22–23 April 1970, *Benedict s.n.* (holotype: SBBG!; isotype: SBBG!).

Plantae annuae, 8–20 cm altae. Caulis unicus vel e basi aliquot, supra ramosus, ascendens vel arrectus. Folia caulina superna oblanceolata vel ovato-obovata in apice acuta in superficie abaxiali in areis parvis tomentosa in marginibus pinnatim in 2–5 segmenta angusta dentata attenuato-acuta crispata divisa, basin versus interdum integra vel solummodo dentata; folia suprema oblanceolata in marginibus usque regionem apicalem pinnatim brevi-lobata. Capitula sub anthesi 3.4–5.4 mm lata in base plerumque rotundata. Involucrum 7–9.2 mm altum; phyllaria exteriora 10–20, quam phyllaria interiora aliquantum breviora pallido- vel atro-rubra plerumque in apice atriora; phyllaria interior 12–20, viridia vel pallide rubra. Flosculi 20–80; corollae 6–10 mm longae mediocriter flavae; ligulae flosculorum extimorum 2.1–2.7 mm latae, trans involucrem 2.5–4 mm exsertae; stamina 4.3–6 mm longa; ramuli styli 0.2–0.4 mm longi. Fructus 1.3–1.6 mm longus, leniter 5-angulus, uniformiter atro-fuscus. Autogamae et aptae se pollinare.

Plants annual, 8–20 cm tall. Stems one to several from the base, branched above, ascending to erect, pale red to deep red. Upper cauline leaves oblanceolate to ovate-obovate, apically acute, abaxial surface tomentose in patches, margins pinnately parted into 2–5 narrow, toothed, attenuate-acute, crisped segments, basally sometimes entire or only toothed; uppermost leaves oblanceolate, margins pinnately short lobed to near the apex. Heads 3.4–5.4 mm wide at anthesis, base generally rounded. Involucre 7–9.2 mm high; outer phyllaries 10–20, nearly as long as inner phyllaries, pale red to dark red, tips generally darker; inner phyllaries 12–20, green to pale red. Florets 20–80; corollas 6–10 mm long, medium yellow; ligules of outermost florets 2.1–2.7 mm wide, exserted 2.5–4 mm beyond involucre; stamens 4.3–6 mm long; style branches 0.2–0.4 mm long. Fruit 1.3–1.6 mm long, somewhat 5-angled, evenly dark brown. Self-compatible and self-pollinating.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Ventura Co., Anacapa Island, east island, east portion, n-facing slope, e of Lighthouse, 22–23 April

1970, *Benedict s.n.* (SBBG); east island, 25 April 1959, *Blakley 277* (SBBG); west island, n slope of hill between Frenchman's Cove and e end, 31 March 1962, *Blakley 4940* (SBBG, DHL); east island, rare on flats just north of road between Ranger's residence and lighthouse, 23 August 1978, *Junak and Hochberg s.n.* (SBBG)*; west island near Frenchies Cove, 5 June 1962, *Davis 171* (DHL)*; west island, near ridge on steep slope above landing, north side (Frenchman's Cove), 70 ft, 11 May 1963, *Piehl 63268* (DHL, SBBG).

Only self-compatible plants were found in progenies from wild seed, and from intrataxon crosses. A majority of the plants were also strongly self-pollinating (mean percentage of filled/pigmented achenes from undisturbed heads 70%).

1b. *Malacothrix foliosa* A. Gray ssp. *foliosa*

Plants annual, 4–45 cm tall. Stems generally one from the base, generally erect, glabrous, pale-green to red-tinged. Uppermost cauline leaves ovate to lanceolate, pinnately parted at the base into 1–2 long, narrow segments, margins of the distal $\frac{2}{3}$ entire. Heads 3.1–6.7 mm wide at anthesis, base tapered. Involucre 7–11 mm high; outer phyllaries 9–19, generally half the length of inner phyllaries, reddish green, tips dark red; inner phyllaries 13–22, pale green to reddish. Florets 50–120; corollas 10–17 mm long, light yellow; ligules of outermost florets 2–4 mm wide, exserted 5–10 mm beyond the involucre; stamens 5.3–8.1 mm long; style branches 0.3–0.7 mm long. Fruit 0.9–1.5 mm long, medium to dark brown, generally evenly 15-ribbed. Self-compatible or self-incompatible.

Representative specimens (* progenies from wild achenes propagated in growth chambers). USA, California, Los Angeles Co., San Clemente Island, vicinity of Mosquito Harbor, 6 July 1931, *Abrams and Wiggins 339* (CAS, DS, GH, UC); on a north slope, China Point, 9 June 1962, *Blakley 5191* (CAS, SBBG); Wilson Cove, 10 June 1962, *Blakley 5220* (CAS SBBG)*; Wilson Cove, above and n of Seal Cove, 10 June 1962, *Blakley 5234* (SBBG); sand dune area, nw side of island, 15 May 1985, *Davis 457* (DHL)*; along road to Eel Point, 15 May 1985, *Davis 458* (DHL)*; slopes above Eel Point, 15 May 1985, *Davis 459* (DHL)*; southeast point, 2 April 1939, *Dunkle 7211* (DS, LAM, SBBG, UNM); Camp Mesquite, 4 July 1919, *Knoche 982* (DS); sandy beach due west of Wall 2, 11 April 1962, *Raven 17279* (CAS, DS, SBBG, SD, RSA, UC)*; second canyon s of Seal Cove, 8 May 1962, *Raven 17606* (RSA)*; Wilson Cove, 11 April 1962, *Raven 17291* (RSA, UC)*; Wilson Cove, 8 May 1962, *Raven 17625* (RSA, SBBG, SD, UC)*; e end of Northwest Harbor, 100 ft, 12 July 1962, *Raven 18026* (RSA)*; n of Eel Point, *Ross 5442* (SBBG)*; west cove, sw of new landing field, *Ross 5080* (SBBG)*; China Point, 12 April 1973, *Thorne*

42908 (RSA); dunes near Flasher, nw part of island, 10–15 ft, 11 April 1973, *Thorne 42879* (CAS, TEX)*; north end, east coast, 9 April 1923, *Munz 6612* (POM, UC). MEXICO: Baja California Norte. Los Islas Coronados, 12 May 1895, *A. W. Anthony s.n.* (UC); 10 June 1926, *M. E. Jones s.n.* (POM); 30 May 1926, *W. M. Pierce s.n.* (POM, specimen on the left).

In cultivation, 19% of the plants grown from wild achenes were self-incompatible. Self-compatible plants were poorly self-pollinating (<40% of the achenes were filled/pigmented in undisturbed heads. *Malacothrix foliosa* was collected on Los Coronados Island in the past, but not since 1926.

1c. ***Malacothrix foliosa*** A. Gray ssp. ***philbrickii*** W. S. Davis ssp. nov.—TYPE: USA, California, Santa Barbara Co., Santa Barbara Island, west side, 100 m, 27 April 1941, *Moran 824* (holotype: DS!; isotypes: CAS!, UC!, US!).

Plantae annuae, 6–35 mm altae. Caulis unicus vel e basi aliquot, supra ramosus decumbens ascenden vel arrectus. Folia superna caulina ovato-obovata vel lanceolato-oblancheolata, in marginibus vel dentata, longi-serrata vel pinnatim lobata vel in 2–4 paria segmentorum dentatorum plerumque non crispatorum divisa; folia supremus lanceolato-oblancheolata, apicem versus acuta vel obtusa, in marginibus dentata vel apicem versus brevi-lobata. Capitula sub anthesi 3.1–6.7 mm lata, in base subcontacta. Involucrum 7–11 mm altum; phyllaria exteriora 9–19, phyllariis interioribus 2plo vel aliquantum breviora, pallide viridia vel rubrescenti-viridia, in apice subatriora et squarrosa; phyllaria interiora 11–21, subviridia vel viridia. Flosculi 40–113; corollae 8–16 mm longae, mediocriter flavae; ligulae flosculorum extimorum 2–4 mm latae trans involucrum 4–8 mm exsertae; stamina 5–8 mm longa; ramuli styli 0.4–0.7 mm longi. Fructus 1.3–1.7 mm longus, mediocriter vel atro-fuscae, plerumque 5-angulus. Autogamae vel non autogamae.

Plants annual, 6–35 cm tall. Stems one to several from the base, branched above, decumbent, ascending to erect. Upper cauline leaves ovate-obovate to lanceolate-oblancheolate, margins dentate, long-serrate, or pinnately lobed or parted into 2–4 pairs of toothed, generally not crisped segments; uppermost leaves lanceolate-oblancheolate, apically acute to obtuse, margins toothed or short lobed to near the tip. Heads 3.1–6.7 mm wide at anthesis, base somewhat tapered. Involucre 7–11 mm high; outer phyllaries 9–19, ½ as long to nearly as long as inner phyllaries, pale green to reddish green, tips generally darker, and squarrose; inner phyllaries 11–21, pale green to green. Florets 40–113; corollas 8–16 mm long, medium yellow; ligules of outermost florets 2–4 mm wide, exserted 4–8 mm beyond involucre; stamens 5–8 long; style branches 0.4–0.7 mm

long. Fruit 1.3–1.7 mm long, medium to dark brown, generally 5-angled. Self-compatible or self-incompatible.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Santa Barbara Co., Santa Barbara Island, Cliff Canyon, 5 May 1963, *Blakley 5696* (SBBG, RSA); bluff, due w of mouth of Cliff Canyon, 200 ft, 21 May 1966, *Philbrick and Benedict B66–373* (SBBG)*; bluff, halfway between Landing Cove & Cliff Canyon, 21 May 1966, *Philbrick and Benedict B66–371* (SBBG)*; canyon between Landing Cover and Cliff Canyon, 18 March 1968, *Philbrick B68–32* (CAS, SBBG); lower Middle Canyon, 22 March 1970, *Philbrick and Benedict 70–53* (SBBG); upper part of Graveyard Canyon, 27 April 1968, *Thorne 37512* (RSA); 3 July 1931, *Abrams and Wiggins 304* (DS, UC); above landing, along steps leading to Ranger's Residence, 3 July 1982, *Davis 434* (DHL)*; cliffs above Graveyard Canyon, 3 July 1982, *Davis 435* (DHL)*; upper southern margins of Middle Canyon, 3 July 1982, *Davis 436* (DHL)*; dry ridge along trail n of Ranger's Residence, 3 July 1982, *Davis 437* (DHL)*; along trail s of Middle Cliff Canyon, 3 July 1982, *Davis 438* (DHL)*; along path through desert pavement area, nw tip of island, 3 July 1982, *Davis 439* (DHL)*; west side, common, 28 May 1939, *M.B. Dunkle 8133* (DS, LAM, SBBG, UNM); just above landing platform, Landing Cove, 21 May 1966, *Philbrick and Benedict B66–356* (SBBG); east side of embayment of Cat Canyon, 28 April 1968, *Thorne 37485* (CAS, DS, RSA); north slope of Signal Peak, 4 May 1963, *Blakley 5677* (SBBG).

PHI is particularly variable in growth habit and cauline leaf morphology, and at least two distinct ecotypes are recognizable. On the windy northwest side of Santa Barbara Island, on open flats with coarse, gravelly soil, is a low-growing decumbent form with 5–10 abundantly leafy stems from the base. On the drier southeast side, in among shrubs and other vegetation in small canyons or draws, is an erect form, generally with a single stem from the base and branched above, with cauline leaves reduced upward. The two ecotypes breed true in cultivation and are indistinguishable in floral morphology.

Thirty-one percent of the plants of PHI grown in cultivation from wild achenes were self-incompatible. Self-compatible plants were poorly self-pollinating (<10% of the achenes from mature undisturbed heads were pigmented/filled).

- 1d. ***Malacothrix foliosa* ssp. *polycephala*** W. S. Davis ssp. nov.—
TYPE: USA, California, Ventura Co., San Nicolas Island, annual, pale yellow flowers, clay slopes about 200–300 ft elevation, above the docks scattered near the west end of the island;

colonial San Nicolas Island, 24 April 1966, *Raven and Thompson 20784* (holotype: MO; isotypes: CAS!, DHL!, DS!, JEPS!, NY, OBI!, SBBG!, UC!, US!).

Plantae annuae, 10–35 mm altae. Caulis plerumque e basi unicus, supra ramosus, ascendens vel arrectus, pallide vel mediocriter ruber. Folia superna caulina ovata, in marginibus pinnatim in 3–4 segmenta angusta plerumque dentata non crispata divisa; folia suprema triangularia, basem versus in 1–2 paria segmentorum longorum angustorum divisa, in marginibus partis $\frac{2}{3}$ distalis integra. Capitula sub anthesi diametro 2–4.5 mm, in base subcontracta. Involucrum 5–7 mm altum; phyllaria exteriora 7–15, plerumque phyllariis interioribus longitudine 2plo breviora, rubra in apice et atriora; phyllaria interiora 8–14 subrubra. Flosculi 15–17; corollae 5.3–9 mm longae mediocriter flavae; ligulae flosculorum extimorum 1.5–3.3 mm latae, trans involucrum 1.5–3.5 mm exsertae; stamina 2.9–5 mm longa; ramuli styli 0.4–0.5 mm longi. Fructus 0.9–1.3 mm longus mediocriter vel atrofuscae plerumque aequaliter 15-costatus. Autogamae et aptae se pollinare.

Plants annual, 10–35 cm tall. Stems generally solitary from the base, branched above, ascending to erect, pale red to medium red. Upper cauline leaves ovate, margins pinnately parted into 3–4 narrow, often toothed, not crisped segments; uppermost leaves triangular, parted near the base into 1–2 pairs of long narrow segments, margins of distal $\frac{2}{3}$ entire. Heads 2–4.5 mm wide at anthesis, base somewhat tapered. Involucre 5–7 mm high; outer phyllaries 7–15, generally $\frac{1}{2}$ the length of the inner, red with darker red tips; inner phyllaries 8–14, reddish. Florets 15–70; corolla 5.3–9 mm long, medium yellow; ligules of outermost florets 1.5–3 mm wide, exserted 1.5–3.5 mm beyond the involucre; stamens 2.9–5 mm long; style branches 0.4–0.5 mm long. Fruit 0.9–1.3 mm long, medium to dark brown, generally evenly 15-ribbed. Self-compatible and self-pollinating.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Ventura Co., San Nicolas Island, flats above ravine area between Tranquility Beach and Corral Harbor, 30 May 1986, *Davis 468* (DHL)*; above Tranquility Beach near NAVFAC, 30 May 1986, *Davis 469* (DHL)*; along Tufts Road, 30 May 1986, *Davis 470* (DHL)*; near triangulation point east of Tule Creek, 11 June 1969, *Philbrick and Benedict B69-184* (SBBG); west Jehemy Beach, 10 June 1969, *Philbrick and Benedict B69-171* (SBBG); mesa, between Celery Creek and pond, 10 June 1969, *Philbrick and Benedict B69-135* (SBBG); between Elephant Seal and Dutch Harbor, 24 April 1966, *Raven and Thompson 20784* (DHL, CAS, etc.); near w end of island, 24 April 1966, *Raven and Thompson* (DHL, etc.)*; Sewage Canyon, 12 March 1977, *Smith s.n.*

(DHL)*; near center of the island, 13 March 1977, *Smith s.n.* (DHL)*; near mouth of Celery Canyon, 28 July 1965, *Forman 80* (US); west of Tule Canyon, 4 July 1978, *Wier and Beauchamp s.n.* (UC); area on the ridge, April 1897, *Trask 108* (MO, UC, US).

Only self-compatible plants were found in progenies from wild seed or from intrataxon crosses. A majority of plants were strongly self-pollinating (>70% of the achenes in undisturbed heads were pigmented/filled).

Because of natural hybridization between INC and POL, it is becoming difficult to distinguish between pure POL and hybrid plants in some areas on San Nicolas Island, particularly on the north-west or west sides adjacent to the ocean.

2. *Malacothrix indecora* Greene. Bulletin of the California Academy. 2:152. 1886.—*Malacothrix foliosa* var. *indecora* E. Williams, American Midland Naturalist 58:507.—TYPE: USA, California, Santa Barbara Co., Santa Cruz Island, July and August 1886, *E. L. Greene s.n.* (holotype: CAS!; isotypes: DS!, GH!, MO!, ND-G!, NY!, UC!, US!).

Plants annual, 2–15 cm tall, generally mat-like. Stems several from the base, branched above, green to pale red, essentially glabrous, arachnoid in leaf axiles. Basal leaves obovate, 2–5 cm long, 0.5–1 mm wide, somewhat fleshy, obtusely 4–8-lobed. Cauline leaves similar to basal leaves but somewhat reduced upward. Heads 2–7 mm wide at anthesis, base rounded. Involucre 6–8 mm high; outer phyllaries 22–32, generally ovate, nearly as long as the inner, 1.1–4.2 mm long, 0.4–1.7 mm wide, green to red-tinged, slightly constricted below the obtuse tip, hyaline/scarious margins <0.3 mm wide; inner phyllaries 19–23, linear-lanceolate, 5.2–7.2 mm long, 1–1.8 mm wide, green, tips of alternate ones often paler green, hyaline/scarious margins <0.3 mm wide. Florets 22–81; corolla 4–8 mm long, greenish yellow; ligules of outermost florets 1.5–2.5 mm wide, exserted 1.3–3.3 mm beyond the involucre; stamens 3.4–5.4 mm long; style branches 0.2–0.5 mm long. Fruit 1.2–1.6 mm long, narrowed at the base, the apex truncate and slightly constricted, dark brown, 15-ribbed and 5-angled; outer pappus none. Self-compatible, and self-pollinating. $2n=14$.

Representative specimens (* progenies from wild achenes propagated in growth chambers). USA, California: Santa Barbara Co., San Miguel Island, Twin Harbor on indian mound, 18 July 1939, *Williams 87* (POM); mesa above sea, 19 April 1932, *Hoffmann 692* (UC); n of mouth of Willows Canyon, 19 April 1932, *Hoffmann 694* (UC, LL); rocky knoll opposite Prince's Island, 19 April 1932, *Hoffmann s.n.* (SBBG); seaward edge of coastal flats just n of mouth of Willow Canyon, ca. 50 ft, 20 July 1995, *Junak and Williams*

6061 (SBBG)*; rocky bench just e of Cuyler Harbor, s of e end of Prince Island, ca. 20 ft, 20 July 1995, *Junak and Williams 6057* (SBBG)*. Santa Cruz Island, Black Point, 9 March 1980, *Junak SC-262* (DHL, SBBG)*; Black Point, 19 June 1980, *Junak SC-312* (SBBG)*. Santa Rosa Island, bluff on w side of mouth of Canada Lobos, 10 m, *D. H. Wilken 15219* (SBBG, DHL).

All of the plants grown in cultivation were self-compatible, but poorly to moderately self-pollinating (10–50% filled/pigmented achenes in undisturbed heads). On Santa Cruz Island *M. indecora* is restricted to soils derived from metamorphic and igneous rocks (Junak et al. 1995), and on San Miguel Island it is restricted to coastal flats on soils derived from igneous rocks.

3. *Malacothrix insularis* E. L. Greene, Bulletin of the California Academy of Sciences. 1:194. 1985.—TYPE: MEXICO, Baja California Norte, Coronados Island, May 16, 1885, *Edward L. Greene s.n.* (holotype: CAS!; isotypes: CAS!, DS!, UC!, US!).

Plants annual, 10–45 cm tall. Stems one, or less often several from the base, branched above, ascending or erect. Basal leaves lanceolate-ob lanceolate, 5–12 cm long, 10–25 mm wide, divided-pinnatifid, the lobes narrowly triangular with entire margins, and apically acute; cauline leaves lanceolate to narrowly ovate, reduced upward, the basal $\frac{1}{2}$ pinnately 1–3 parted into narrow, attenuate acute segments, the distal $\frac{1}{2}$ with entire margins. Heads 7–10 mm wide at anthesis, base rounded. Involucre 10–12 mm high; outer phyllaries 20–27, broadly lanceolate to ovate, or spatulate, 3–5 mm long, 2–2.5 mm wide, the midvein generally dark red, hyaline/scarious margins 0.5–1.0 mm wide; inner phyllaries 20–25, linear-lanceolate, 6–8 mm long, 1–1.5 mm wide, hyaline/scarious margins 0.3–0.5 mm wide, central midvein generally dark red; receptacle with thin, short, naked bristles <1.4 mm long; florets 35–160; corollas 10–15 mm long, yellow; ligules of outermost florets 2–2.5 mm wide, exerted 4–6 mm beyond the involucre; stamens 6–9 mm long; style branches 0.6–1.1 mm long. Fruit 2.0–2.6 mm long, the apex slightly constricted, 15-ribbed with 5 ribs more prominent than the others, but the apices not extended beyond lesser ribs at the apex, brown to tan in color; outer pappus a ring of scarious, triangular or needle-like teeth interspersed with 1–3 unbarbed persistent bristles to 5 mm long. $2n =$ unknown.

Specimens examined. MEXICO, Baja California Norte: Los Coronados Island, 30 May 1926, *W.M. Pierce s.n.* (POM, specimen on the right); west slope in southern part of South Island, 8 May 1976, *Moran 23158* (RSA, SD, SBBG).

Living material of INS was not available, but pollen stainability

of herbarium specimens was 70–100%. Pollen was 4–6-pored, and modally larger in diameter than the pollen of either of the two known polyploids (SQU and JUN). It is likely, therefore that INS is polyploid. The most recent collection, by Reid Moran in 1976, reported a single colony of about 100 individuals on steep west slopes in the southern part of the south islet (listed in field notes as *M. coulteri*).

4. ***Malacothrix junakii*** W. S. Davis sp. nov.—TYPE: USA, California, Ventura Co., Anacapa Island, middle island, west-facing slope with *Coreopsis gigantea*, *Eriogonum grande*, extreme tip of Sea Arch Peninsula, distal from Arch, 2 June 1978, *Philbrick B78-327* (holotype: SBBG!, top left specimen; isotype: DHL!).

Plantae annuae, 5–30 cm altae. Caulis unicus vel aliquot e radice palari oriens, supra ramosus, ascendens vel arrectus, viridis vel mediocriter ruber, glaber. Folia basalia 4–10 cm longa, 5–20 mm lata, oblanceolata, in dimidio distali dentibus 2–3 vel lobis pinnatis 2–4 in segmenta brevia obtusa divisis instructa. Folia caulina late lineari-lanceolata, pinnatim 2–4-lobata, lobis angustis et longitudine subaequalibus praedita; folia superna in base in 1–2 segmenta angusta acuta pinnatim divisa, in marginibus partis $\frac{2}{3}$ distalis integra. Capitula sub anthesi 3–6 mm lata, in base rotundata; involucrem 7–8.5 mm altum; phyllaria exteriora 7–11, lanceolata vel ovata, 1.2–3.5 mm longa, 1–1.5 mm lata, plerumque phyllariis interioribus 2plo breviora, viridia vel rubro-tincta, marginibus hyalinis scariosis <0.3 mm latis instructa; phyllaria interiora 9–13, lineari-lanceolata, 5–7 mm longa, 1–1.6 mm lata, acuta. Receptaculum setis paucis gracilibus nudis <0.6 mm longis armatum. Flosculi 20–85; corollae 7–11 mm longae mediocriter flavae; ligulae flosculosum extimorum 1.4–2 mm latae, trans involucrem 3.5–5.5 mm exsertae; stamina 5–6.2 mm longa; ramuli styli 0.4–0.7 mm longi. Fructus 1.6–2 mm longus, cylindrico-fusififormis, in base angustior quam in apice subconstricto truncato, plerumque atro-fuscus, aequaliter 15-costatus vel leniter 5-angulus; pappus exterior dentibus perbrevibus irregularibus armatus e setis 1–2 persistentibus nudis usque 4 mm longis compositus. Autogamae.

Plants annual, 5–30 cm tall. Stems one to several from a taproot, branched above, ascending to erect, green to medium red, glabrous. Basal leaves 4–10 cm long, 5–20 mm wide, oblanceolate, distal $\frac{1}{2}$ with 2–3 teeth, or pinnately 2–4-lobed with short, obtuse segments. Cauline leaves broadly linear-lanceolate, pinnately 2–4-lobed, lobes narrow and approximately equal in length; uppermost leaves pinnately 1–2-parted at the base into narrow, sharp segments, margins of the distal $\frac{2}{3}$ entire. Heads 3–6 mm wide at anthesis, base rounded; involucre 7–8.5 mm high; outer phyllaries 7–11, lanceolate to ovate, 1.2–3.5 mm long, 1–1.5 mm wide, generally $\frac{1}{2}$ as long as inner

phyllaries, green to red-tinged, hyaline scarious margin <0.3 mm; inner phyllaries 9–13, linear-lanceolate, 5–7 mm long, 1–1.6 mm wide, acute. Receptacle with few thin, naked bristles <0.6 mm long. Florets 20–85; corollas 7–11 mm long, medium yellow; ligules of outermost florets 1.4–2 mm wide, exerted 3.5–5.5 mm beyond the involucre; stamens 5–6.2 mm long; style branches 0.4–0.7 mm long. Fruit 1.6–2 mm long, the base narrower than the slightly constricted truncate apex, generally dark brown, equally 15-ribbed or somewhat 5-angled; outer pappus of very short irregular teeth and 1–2 persistent naked setae to 4 mm long. Self-compatible. $2n=28$.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Ventura Co., Anacapa Island, moist sheltered pocket, 19 May 1928, *Howell 3795* (CAS); middle island, Lavatera Cove, ca. 75 ft, 23 April 1982, *Junak MA-60* (SBBG)*; middle island, slopes above East Fish Camp, on east edge of major gully running down to shoreline, south side of island, rare on open south-facing slope, 80 ft, 29 April 1986, *Junak MA-145* (DHL, SBBG)*; middle island, onshore slope, at foot of Sea Arch Peninsula, west of Sheep Camp, localized on flats and adjacent coastal bluffs, 80 ft, 22 April 1986, *Junak MA-105* (DHL, SBBG)*.

5. *Malacothrix squalida* Greene, Bulletin of the California Academy of Sciences 2:152. 1886.—*Malacothrix foliosa* var. *squalida* E. Williams, American Midland Naturalist 58:507. 1957.—*Malacothrix insularis* var. *squalida* Ferris, Contributions from the Dudley Herbarium 5:102. 1958.—TYPE: USA, California, Santa Barbara Co., rocky promontory above Prisoner's Harbor, Santa Cruz Island, July and August 1886, *E.L. Greene s.n.* (holotype: CAS!; isotypes: DS!, ND-G!, NY!, UC!).

Plants annual from a taproot, 4–30 cm tall. Stems generally several from the base. Basal leaves oblanceolate, 4–14 cm long, 10–25 mm wide, with teeth or narrow, toothed sharp lobes. Lower cauline leaves similar to basal leaves but more deeply toothed or lobed; upper cauline leaves ovate to narrowly triangular, with 4–9 narrow, sharp, generally toothed lobes. Heads 6–10 mm wide at anthesis, base rounded. Involucre 9–12 mm high; outer phyllaries 12–26, ovate to broadly ovate, 2.5–7 mm long, 1.8–2.5 mm wide, with dark mid-veins, hyaline/scarious margins 0.5–1 mm wide and irregularly toothed; inner phyllaries 19–23, linear-lanceolate 6–9 mm long, 1.6–2.5 mm wide, green or reddish, hyaline/scarious margins <0.4 mm wide. Receptacle with scattered naked bristles 0.1–0.5 mm long. Florets 30–160; corollas 12–19 mm long, light yellow; ligules of outermost florets 2–3 mm wide, exerted 6–10.5 mm beyond the involucre; stamens 6–9.5 mm long; style branches 0.5–0.7 mm long. Fruit 1.5–2.2 mm long, medium to dark brown, 15-ribbed, 5-angled,

tips of more prominent ribs extended above the lesser ribs at the achene apex; outer pappus of irregular teeth, and no persistent setae (rarely 1). Self-compatible. $2n=28$.

Specimens examined (* progenies propagated from wild achenes in growth chambers). USA, California: Ventura Co., Middle Anacapa Island, at e end of knife edge area, 1 June 1978, *Philbrick and Hochberg B78-288* (SBBG)*; e of knife edge mesa near triangulation point, 12 May 1968, *Piehl 63290* (SBBG); n end of island, 2 July 1931, *Abrams and Wiggins 270* (UC). Santa Barbara Co., Santa Cruz Island. E-facing slope, canyon draining from Coche Point to Potato Harbor, 8 May 1968, *Philbrick, Mcpherson, and Benedict B68-292* (SBBG); 1888, *T. S. Brandege s.n.* (UC).

All of the plants grown in cultivation were self-compatible and strongly self-pollinating (>80% filled-pigmented achenes in undisturbed heads).

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NOTEWORTHY COLLECTIONS

ARIZONA

CENTRANTHUS RUBER (L.) DC. (VALERIANACEAE).—Cochise Co., Bisbee, edge of parkinglot near junction of Main St. and Commerce St., 5400' (1620 m), 14 Oct 1996, *Laferrière* 2679. (ARIZ, ASU).

Previous knowledge. Eurasian species sometimes cultivated as an ornamental. Occasionally established in the wild in California (Munz & Keck, 1959).

Significance. First time reported outside cultivation in Arizona.

SALPICHROA ORIGANIFOLIA (LAM.) BAILLON (SOLANACEAE)—Cochise Co., Bisbee, unkempt lawn at 129 Tombstone Canyon Road, 5400' (1620 m), 14 Oct 1996, *Laferrière* 2678 (ARIZ, ASU, MO).

Previous knowledge. Argentine species sometimes cultivated as an ornamental. Occasionally known from the wild in California and Florida but rarely producing fruit in North America (D'Arcy, MO, pers. comm.). The related *S. rhomboidea* (Gill. & Hook.) Miers is a difficult weed in parts of California (Munz & Keck, 1991).

Significance. First time reported outside cultivation in Arizona.

—JOSEPH E. LAFERRIERE, Herbarium, 113 Shantz Building, University of Arizona, Tucson AZ. 85721.